Marine Biology (2023) 170:101
https://doi.org/10.1007/s00227-023-04236-x

SHORT NOTES

Stomach content analysis of North Sea cephalopods: often-overlooked predators with direct impact on commercially used fish species?

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Received: 1 February 2023 / Accepted: 16 May 2023 / Published online: 5 July 2023

Abstract
The study of marine food web models has increased during the last years, but input data of important groups such as cephalopods are missing sometimes which restricts the quality of the model results. Cephalopods feed on a variety of preys, ranging from small crustaceans to large commercially important fish species. In turn, they are taken by larger invertebrates, fish, cephalopods, marine mammals and seabirds, which emphasizes their important role in various marine food webs. Our study presents stomach content analyses of various cephalopod species from the North Sea and describes their general feeding trends. The results further support the inclusion of cephalopods as predators into food web models to increase our knowledge of the North Sea ecosystem and to improve its management. Our data in combination with observed increasing biomasses of North Sea cephalopods suggest that the impact of cephalopods in the North Sea food web has increased and that large-sized cephalopods have become more important as predators for commercially exploited fish species during recent years.

Keywords Food web · Stomach content · Loliginidae · Ommastrephidae · Sepiidae · Squid

Introduction

Cephalopods play a significant role in coastal and oceanic food webs. On the one hand, cephalopods are active predators, taking a wide variety of preys; on the other hand, a lot of large marine predators feed upon cephalopods (Nixon 1987; Clarke 1996; Rodhouse and Nigmatullin 1996; Boyle and Rodhouse 2005; Gasalla et al. 2010). However, studies on the feeding ecology of cephalopods are rare in the North Sea (Bobowski et al. 2023), one of the most productive shelf areas of the NE Atlantic, and focus on longfin squid (Loliginidae) emphasizing the potential impact of *Loligo forbesii* and *L. vulgaris* on different components in the food web (Collins et al. 1994; Collins and Pierce 1996; Pierce et al. 1994; Wangvoralak et al. 2011). These studies show that the prey varies between areas and species and emphasizes that regional and species-specific food web studies are necessary. The North Sea ecosystem suffers dramatic changes as a response to climate and anthropogenic pressures. This causes changes in abundance and distribution of fish and cephalopod species which form important components of the North Sea ecosystem (e.g.,Perry 2005; Engelhard et al. 2014; Oesterwind et al 2022).

The rising complexity of available food web models provides the inclusion of increasing numbers of taxonomic groups. However, limited knowledge of the trophic ecology of cephalopods weakens their consideration in these models (Lishchenko et al. 2021; Bobowski et al. 2023), and consequently a better understanding of the whole North Sea ecosystem.

To analyze the trophic ecology of cephalopods, various modern techniques have been applied more recently which include DNA-based diet analysis as well as stable isotope or fatty acid analysis (e.g.,Braley et al. 2010; Pethybridge et al. 2011; Roura et al. 2012; Merten et al. 2017). However, the classical analysis of investigating stomach contents is still an important tool to study the animal's food and its trophic ecology. The advantages compared to modern techniques are obvious: amongst others, it is possible to identify the prey items to species level and to estimate the prey size (e.g. by published regressions for fish otoliths and bones,

Responsible Editor: R. Villanueva.

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or cephalopod beaks), both being key issues in food web models.

In the present study, we performed classical stomach content analyses of the twelve most prominent North Sea cephalopods. Our study will (i) increase our knowledge in the trophic ecology of North Sea cephalopods with substantial information for food web models and (ii) provide information if and which North Sea cephalopods have the potential to impact commercially used fish species.

Materials and methods

Sampling

All species were sampled in the North Sea during ICES International Bottom Trawl surveys (IBTS) in winter (January/February) 2008, 2009 and 2010, and from German Small-Scale Bottom Trawl surveys (GSBTS) as well as IBTS in summer (July/August) 2007, 2008 and 2009. Sampling of both surveys followed ICES IBTS standards (ICES 2006). A random subsampling of cephalopods was taken for stomach content analysis and immediately frozen on board.

Stomach content analysis

In the lab, the samples were thawed and dorsal mantle length (DML) was measured to the nearest 1 mm for each animal. Only filled stomachs were dissected and the contents were washed through a sieve with a mesh size of 0.25 mm. Prey items were identified by a binocular to the lowest possible taxon following the guides of Clarke (1986), Watt et al. (1997), Leopold (2001) and Svetocheva et al. (2007). After otoliths and vertebrae had been identified to species level, minimum and maximum sizes were estimated for each fish with the support of the literature mentioned above. Presence of all identified prey items was documented.

Data analysis

The frequency of occurrence of identified prey items was calculated as the percentage of stomachs, in which the prey item occurred out of the total number of stomachs examined (prey fraction). Prey fraction was related to cephalopod size classes (DML) and estimated prey size (fish only) to DML and season (summer and winter). Figures were created in Excel and R-statistic (R Development Core Team 2009), whilst statistics were performed in SigmaStat (Systat Software Inc.). In order to compare the lengths of fish prey by season, the smallest calculated fish length from the individual stomachs of the respective species of the individuals fished in summer was compared with those from winter, and the same for the largest estimated fish prey. In all cases, the Normality Test failed (Shapiro–Wilk) and a Mann–Whitney Rank-Sum test was performed.

Results

The identified prey items show a high variation and are described for the different species in the following.

Loliginidae

Alloteuthis spp. (*Alloteuthis subulata*—European common squid, *A. media*—Midsize squid)

A total of 484 stomachs of *Alloteuthis* spp. from winter samples were investigated, including 224 (46%) stomachs with crustaceans, 147 (30%) with fish, 62 (13%) with chaetognaths, 52 (11%) with cephalopods and 3 (<1%) with polychaetes remains, whilst the stomach content of 68 *Alloteuthis* spp. was not identifiable (Tab. 1). A total of 251 stomachs from summer samples were analyzed of which 180 (72%) stomachs contained fish, 112 (45%) crustaceans, 31 (12%) cephalopods 4 (2%) chaetognaths and 3 (1%) polychaetes remains, whilst the stomach content of 15 individuals was not identifiable. *Alloteuthis* spp. showed a significant relation between squid size (DML) and prey composition (share of major taxonomic groups), which explained the difference between summer and winter prey compositions, and prey size as summer DML of *Alloteuthis* sp. was lager compared to winter (Table 1). Young and small-sized squid feed mainly on crustaceans whilst for larger sized squid fish is becoming a more important prey (Fig. 1).

In summer, the calculated mean minimum length of fish prey was 14 mm ($\pm$ 8 mm) whilst the estimated mean maximum length was 30 mm ($\pm$ 11 mm) and thus significant smaller ($p \leq 0.001$) than the mean minimum length (31 mm, $\pm$ 11 mm) and mean maximum length (50 mm $\pm$ 13 mm) in winter (Fig. 2). The largest identified fish in winter and summer was a gobiid with a similar maximum length of 72 and 70 mm, respectively. Amongst the cephalopod prey, *A. subulata* and *L. forbesii* were identified in a few stomachs.

Loligo forbesii—European northern squid

Stomach contents were investigated in 253 individuals of *L. forbesii* caught in summer and in 256 individuals caught in winter. In summer, 176 stomachs (70%) contained crustaceans, 155 fish (61%), 14 chaetognaths (6%), 3 polychaetes (1%) and 1 cephalopod (<1%), whilst the stomach contents of 3 individuals were not identifiable (Table 1). In winter, fish was present in 171 (67%) stomachs, crustaceans in 55 (22%), cephalopods in 53 (21%), chaetognaths in 8 (3%) and

Table 1 Number of stomach contents per species and season, mean DML ± standard deviation per species and season, and numbers of stomachs containing higher taxonomic groups in bold (except polychaetes) and fish species of individuals which were sampled during NS-IBTS 2007–2010

Species	*L. forbesii*		*L. vulgaris*		*Alloteuthis* spp.		*I. coindetii*		*T. eblanae*		*T. sagittatus*		*R. macrosoma*	*S. oweniana*
Season	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Winter
Non-empty stomachs (n)	256	253	58	1	484	251	28	6	44	47	29	5	16	15
Mean DML ± SD (mm)	184.0 (±92.4)	85.0 (± 35.8)	202.1 (±69.5)	42.0	61.6 (±15.6)	76.3 (±18.4)	82.2 (±48.1)	141.5 (±38.9)	75.2 (±29.9)	134.0 (±25.5)	295.7 (±53.0)	337.6 (±75.4)	32.2 (±10.9)	28.3 (±7.8)
Cephalopoda	**53**	**1**	**6**	**0**	**52**	**31**	**11**	**1**	**16**	**2**	**15**	**1**	**1**	**1**
Crustacea	**55**	**176**	**1**	**1**	**224**	**112**	**7**	**2**	**2**	**3**	**5**	**0**	**9**	**11**
Chaetognatha	**8**	**14**	**0**	**0**	**62**	**4**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
Pisces	**171**	**155**	**51**	**0**	**147**	**180**	**11**	**3**	**21**	**35**	**16**	**3**	**4**	**6**
Pisces unident	84	29	30		60	24	10		15	16	8	2	3	5
Argentiniformes														
Argentinidae spp.	1													
Argentina sphyraena	3								1					
Callionymiformes														
Callionymus sp.	1													
Callionymus maculatus	1													
Callionymus lyra	1													
Carangiformes														
Trachurus trachurus		1												
Clupeiformes														
Clupeidae unident	2	3	6			2				1				
Clupea harengus	3	1								1	2			
Sprattus sprattus	1		14					1						
Gadiformes														
Cilliata mustella			1											
Gadidae unident	7	1			1	2			1	1				
Gadiculus argenteus	5													
Gadus morhua	1													
Melanogrammus aeglefinus	2									1				
Merlangius merlangus	5	9	1							2				
Micromesistius poutassou											1			

Table 1 (continued)

Species	*L. forbesii*		*L. vulgaris*		*Alloteuthis* spp.		*I. coindetii*		*T. eblanae*		*T. sagittatus*		*R. macrosoma*	*S. oweniana*
Season	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Winter
Pollachius pollachius	1													
Polachius virens		1												
Trisopterus spp.	18	5						1	3	4	3			
Trisopterus esmarkii	10	1								4				
Gobiiformes														
Gobiidae unident	14	102	1		80	158	1	1	1	4	1	1	1	1
Aphia minuta	1													
Pomatoschistus lozanoi	1					2								
Crystallogobius linearis		5				1				1				
Osmeriformes														
Mallotus villosus	3													
Perciformes														
Ammodytes spp.	10	20	4		7	2				1	1			
Ammodytes tobianus	1													
Pleuronectiformes														
Pleuronectiformes spp.	1													
Hippoglossoides platessoides	1													
Hippoglossus hippoglossus	1	1								1				
Scophthalmus rhombus		1												
Scombriformes														
Scomber scombrus	5													

polychaetes in 2 (< 1%) stomachs, whilst the stomach contents of 14 *L. forbesii* were not identifiable. In larger *L. forbesii*, fish and cephalopod prey were more important than crustacean and chaetognaths prey (Fig. 3). In addition, size of preyed fish increased with dorsal mantle length (Fig. 4), which explained the difference between seasonal prey composition and prey size, because mean DML of examined *L. forbesii* was smaller in summer compared to winter (Table 1).

In summer, a total of nine different fish species from seven different fish families were found. The fish prey mainly consisted of Gobiidae followed by Ammodytidae and Gadidae, whereas Clupeidae, Pleuronectidae, Bothidae and Carangidae were scarce (Table 1). In winter, the identified fish prey consisted of a total of 19 species from nine different families. Gadidae occurred most frequently, followed by Ammodytidae and Gobiidae. Due to larger sizes of *L. forbesii* in winter (Table 1; Fig. 4), fishes preyed upon in summer were significantly ($p \leq 0.001$) smaller in mean length (min. mean 22 mm ± 25 mm; max. mean 42 mm ± 30 mm) compared to fish prey in winter (min mean 100 mm ± 62 mm; max. mean 123 mm ± 63 mm). The largest identified fish in summer samples was a sandeel (Ammodytidae) with a total length of 160 mm, whereas the largest identified fish in winter samples was a herring of 327 mm size. Within the cephalopod prey composition, *L. forbesii* was the most common (indicating cannibalism), followed by *Alloteuthis* spp. Other cephalopods identified in the prey were *L. vulgaris*, *S. atlantica* and *S. oweniana*.

Loligo vulgaris—European squid

A total of 58 stomach contents of *L. vulgaris* from winter specimens and one from summer were investigated. In the single specimen from summer with a DML of 42 mm, only crustacean items were found (Table 1). In winter, in 51 (88%) stomachs occurred fish, in 6 (10%) cephalopods and in 1 (2%) crustacean prey items, whilst the stomach content of 5 individuals was not identifiable. The mean DML of the 51 animals which contained fish prey was 204 mm (± 68 mm), whilst squid feeders with a mean DML of 219 mm (± 41 mm) were larger. The single individual with crustacean items had a DML of 161 mm. *Sprattus sprattus* and other unidentified Clupeidae were the most frequent fish species. Additionally, *Merlangius merlangus*, Gobiidae and *Ammodytes* spp. were identified. Only *L. forbesii* was identified once as cephalopod prey with an estimated DML of 17 mm.

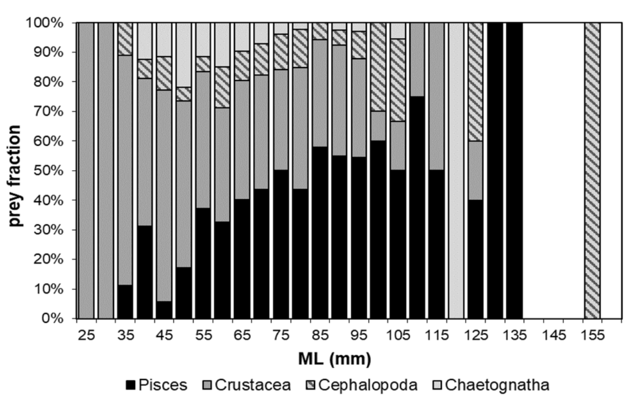

Fig. 1 Relationship between DML of *Alloteuthis* spp. and prey composition

Ommastrephidae

Illex coindetii—Broadtail short-fin squid

In summer, the stomach contents of six *I. coindetii* specimens were analyzed. In three (50%) stomachs, fish occurred, in two (33%), crustaceans and in 1 (17%), cephalopod items, whilst the stomach content of one individual was not identifiable. From the winter samples, the stomach contents of 28 individuals were analyzed. Fish items and cephalopod remains were found in 11 (39%) stomachs, whilst crustacean items were present in seven (25%) stomachs. The stomach contents of five *I. coindetii* specimens were not identifiable. The animals that fed on fish had a mean DML of 100 mm (± 39 mm), followed by squid feeders with a mean DML of 97 mm (± 70 mm). Individuals that fed on crustaceans had the smallest mean DML of 88 mm (± 34 mm). However, a significant difference in DML ($p = 0.468$; Kruskal–Wallis One-Way ANOVA on Ranks) with respect to the prey composition could not be detected, but might be due to the relatively low sample number. One *I. coindetii* with a DML of 312 mm had taken one *L. forbesii* with a DML of 42 mm, and one *I. coindetii* with a DML of 98 mm took one *S. atlantica* (DML: 16 mm).

Todaropsis eblanae—Lesser flying squid

A total of 44 stomach contents of *T. eblanae* from winter and 47 from summer were analyzed. In both summer and winter, fish were most frequently found in the stomachs, followed by crustaceans and cephalopods. In summer, the number of individuals with fish items in the stomach was 35 (75%) and in winter 21 (48%). In winter, cephalopods were found in 16 stomachs (36%) and were more frequent in the stomachs than in summer where they occurred in two stomachs (4%). Crustaceans were found in three individuals in summer (6%) and two in winter (5%). In winter, 12 stomachs and in summer, nine stomachs contained no identifiable food items. The mean DML of animals showing crustacean prey was 102 mm (± 24 mm) and is smaller than the mean DML of fish feeders (112 mm ± 37 mm) but larger than

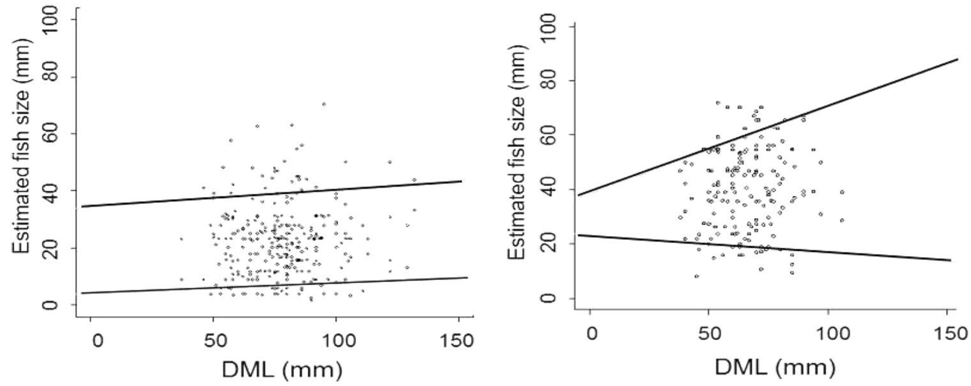

Fig. 2 Relationship between DML of *Alloteuthis* spp. and estimated min and max. fish sizes. The upper and lower lines represent the 90 and 10 quantiles. Left figure: summer, right figure: winter

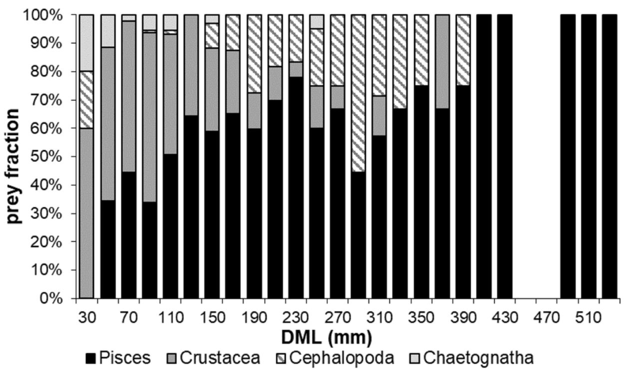

Fig. 3 Relationship between DML of *L. forbesii* and prey composition

that of animals that preyed on cephalopods (mean DML: 73 mm ± 30 mm). In summer, the fish prey was much more heterogeneous, with Gadidae most frequently, and found in 32% of the stomachs. In winter, the proportion of Gadidae was again the highest and occurred in 19% of the stomachs. 71% of the fish prey could not be identified more precisely. The largest identified fish species was a *Clupea harengus* with an estimated size between 131 and 161 mm captured by a *T. eblanae* specimen with a DML of 120 mm. Even with a moderate sample size, fish prey became larger with an increasing DML (Fig. 5), due to seasonal differences in the mean DML of *T. eblanae* with larger specimens in summer than in winter (Table 1).

Todarodes sagittatus—European flying squid

A total of 29 stomach contents of *T. sagittatus* from winter and 5 from summer with a similar ranging DML were analyzed (Table 1). In summer samples, fish remains were identified in three out of five stomachs examined, whilst cephalopods were found in one stomach and unidentifiable remains in another. In winter, the proportion of stomachs with fish items (16 stomachs) and cephalopods (15 stomachs) was almost balanced (55% and 52% respectively). In five stomachs (17%), crustacean remains were found, whilst four stomachs consisted of unidentifiable prey items. *T. sagittatus* that fed on fish were slightly but not significantly larger with a mean DML of 304 mm (± 68 mm) than those that fed on squid (mean DML: 301 mm ± 38 mm). However, both (fish and cephalopod feeders) were significantly ($p \leq 0.05$; Kruskal–Wallis One Way ANOVA on Ranks) larger than individuals that preyed upon Crustaceans (mean DML: 241 mm; ± 40 mm). In summer, only Gobiidae were identified whilst in winter Gobiidae, Ammydytidae, *M. poutassou*, *C. harengus* and *Trisopterus* ssp. were found. The largest fish identified within the stomachs was a herring (*C. harengus*) with an estimated total length between 318 and 354 mm, which was eaten by a *T. sagittatus* with a DML

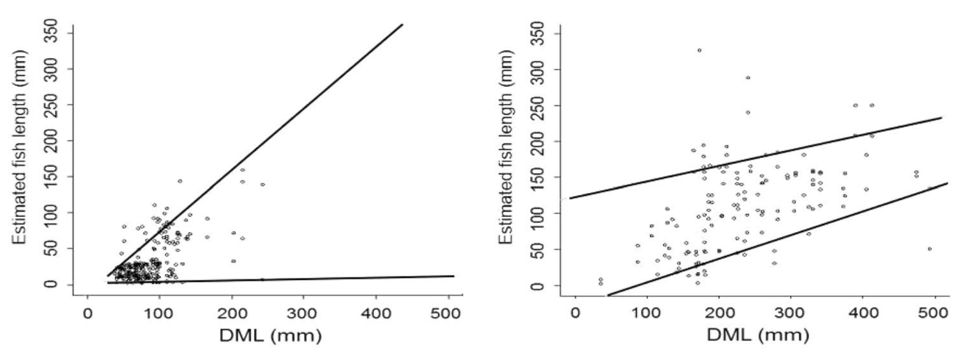

Fig. 4 Relationship between DML of *L. forbesii* and estimated min and max. fish sizes. The upper and lower lines represent the 90 and 10 quantiles. Left figure: summer, right figure: winter

of 490 mm. Based on identified beaks, two *L. forbesii*, two *S. atlantica* and one *Alloteuthis* spp. as well as one *S. oweniana* were identified in the prey of *T. sagittatus*. The estimated DML of those cephalopods ranged from 16 to 38 mm.

Others

Three stomachs of *Eledone cirrhosa* (Horned octopus), fished in summer, were examined. Two of them contained crustaceans, whilst the other contained bivalves.

The stomach contents of twenty-three specimens of *S. atlantica* (Atlantic bobtail squid) caught during winter and with a mean length of 16 mm (± 3 mm) were investigated. In twenty stomachs, crustaceans were identified whilst the stomach content of the remaining three individuals consisted of unidentifiable items. During summer catches, the stomach contents of three *S. atlantica* with a mean DML of 8 mm (± 2 mm) were investigated and consisted of crustaceans.

The stomach contents of fifteen individuals of *Sepietta oweniana* (Common bobtail squid) that were caught in winter with a mean DML of 28 mm (± 8 mm) were investigated (Table 1). Only one stomach contained unidentifiable prey items. Crustacean items were found in eleven (73%) stomachs. Fish was found in six (40%) stomachs and cephalopods in one (7%) stomach. Gobiidae was the only identified fish taxon with length sizes varying between 11 and 41 mm.

Sixteen stomachs of *R. macrosoma* (Stout bobtail squid) with a mean DML of 32 mm (± 11 mm) were examined from the winter samples (Table 1). Nine stomach contents (56%) consisted of crustaceans, four stomachs fish (25%), and in one stomach cephalopod items were found, whilst four stomachs consisted of non-identifiable prey items. Fish items from Gobiidae with a total length between 33 and 43 mm were identified in the stomach (6%) of one *R. macrosoma* (DML of 29 mm).

Two *Sepia elegans* (Elegant cuttlefish) and one *Sepia officinalis* (Common cuttlefish), all fished in winter, were examined. The stomach content of one *S. elegans* consisted of crustacean items and unidentified fish scales, and in the other stomach, only crustacean remains were determined whilst the stomach of *S. officinalis* contained crustaceans.

Discussion

Loliginidae

Alloteuthis spp. (*Alloteuthis subulata*—European common squid, *A. media*—Midsize squid)

Alloteuthis sp. is one of the most abundant cephalopods in the IBTS samples (de Heij and Baayen 2005; Oesterwind et al. 2010). A recent study applying DNA barcoding of the genus *Alloteuthis* suggested that only *A. media* occurs in the North Sea (Sheerin et al. 2023), whereas until recently, it was assumed that two *Alloteuthis* species, *A. subulata* and *A. media* occur in the area (e.g.; Anderson et al 2008; Gebhardt and Knebelsberger 2015). We used the classification *Alloteuthis* spp. to include both species and to make comparisons with older records possible. There is less information in the recent literature on the diet of *Alloteuthis* spp.; however, already Jaeckel (1958) reports that small Atlantic herring (*C. harengus*) and other small schooling fish species were a substantial diet of the squid in the North Sea. In a comprehensive study on the ecology of cephalopods in the German Bight (eastern North Sea), crustaceans were identified in 55% and small fish 45% (mainly Clupeidae, Pleuronectidae and Gadidae) of the stomachs of *Alloteuthis* spp. (Steimer 1993). Further investigations in the central North Sea on stomach contents of *Alloteuthis* spp. revealed that Gobiidae and Clupeidae as well as young squid formed an important diet (Schroeder 1999). Even if *Alloteuthis* sp. is a rather small cephalopod species in the North Sea, it should be considered that it impacts the recruitment of commercially important fishes because it preys upon their small life stages and appears in high abundances (e.g.; de Heij and Baayen 2005; Oesterwind et al. 2010).

Loligo forbesii—European northern squid

Loligo forbesii is the second most abundant squid in the IBTS samples (de Heij and Baayen 2005; Oesterwind et al. 2010). *L. forbesii* feeds on a wide variety of prey including polychaetes, molluscs, crustaceans and fish. Younger and thus smaller *L. forbesii* feed more on crustaceans, whereas the larger ones tend to eat fish. Amongst the fish prey, the most important families are Ammodytidae, Clupeidae, Gadidae and Gobiidae (Collins et al. 1994; Pierce et al.

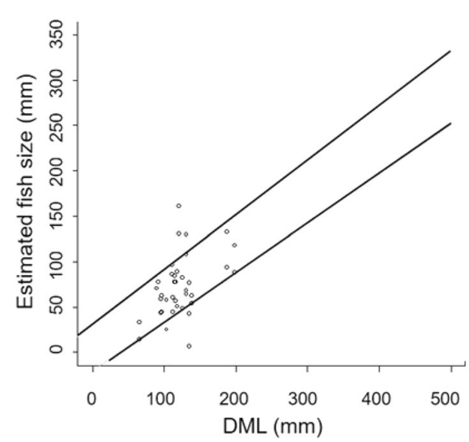

Fig. 5 Relationship between DML of *T. eblanae* and estimated min and max. fish sizes from summer and winter samples. The upper and lower lines represent the 90 and 10 quantiles

1994; Collins and Pierce 1996; Pierce and Santos 1996). The fish preys, described by Pierce et al. (1994) and Collins et al. (1994) in Scottish and Irish waters, respectively (*M. merlangius*, *Trisopterus* spp. Ammodytidae and *S. sprattus*), were also identified in our study, but some with a higher proportion of prey. Furthermore, Collins and Pierce (1996) conclude that cannibalism only occurs in animals with a DML larger than 150 mm, and then animals with a DML between 20 and 50 mm are eaten. The combination of relatively high abundances as well as the results of our study illustrate that *L. forbesii* has a high potential to exert predation pressure on fish species including various commercially used species.

Loligo vulgaris—European squid

Loligo vulgaris is the lowest abundant loliginid in the IBTS samples (de Heij and Baayen 2005; Oesterwind et al. 2010). Pierce et al. (1994) describe that the prey spectrum of *L. vulgaris* is similar to that of *L. forbesii*. Similar to the North Sea, in Spanish waters, prey composition of *L. vulgaris* depends on its DML, with higher importance of crustaceans in the diet of smaller animals than for the larger animals (Rocha et al. 1994). We were not able to identify more than 50% of the fish remains, but *S. sprattus* shows the highest frequency of occurrence in the stomachs, whereas the share of this species in *L. forbesii* was substantially less, and *T. esmarkii* was more frequent in *L. forbesii* than in *L. vulgaris*. However, this difference is less likely due to preferences or different hunting strategies, but rather by the typical distribution of this species with a higher distributional overlap of *L. forbesii* and *T. esmarkii* in northern waters and *L. vulgaris* and *S. sprattus* in southern waters (Oesterwind et al. 2010; ICES 2010). Rocha et al. (1994) also suggest that the prey composition of *L. vulgaris* in Spanish waters mainly depends on the availability of prey. Furthermore, *L. vulgaris* feeds on crustaceans and polychaetes in addition to fish (Guerra and Rocha 1994; Pierce et al. 1994; Rocha et al. 1994), which is also observed in the North Sea. In conclusion, the relatively low abundance of *L. vulgaris* in the North Sea suggests that this species has relatively minor impact on the commercially used fish species but might be substantial on a local scale when abundances become relatively high.

Ommastrephidae

Illex coindetii—Broadtail short-fin squid

The low number of investigated stomach contents in the present study is based on the relatively low occurrence of *I. coindetii* in the North Sea during the last decades (Oesterwind et al. 2015). More recently, a new spawning stock evolved in the northern North Sea (Oesterwind et al. 2020) with an expansion into Skagerrak and Kattegat (Oesterwind and Schaber 2020), and the stock seems to increase substantially so that the species will become more important in the food web of the North Sea. There is no information on the prey composition of *I. coindetii* in the North Sea, but studies from the central East Atlantic suggest that its prey consists mainly of crustaceans, fish and cephalopods (Castro and Hernández-García, 1995). In areas with high *I. coindetii* abundances or low prey abundances, cannibalism has also reported for *I. coindetii* (Dawe 1988). However, the high production of fish in the North Sea makes cannibalism in squid unlikely in that area. Due to the growing numbers of *I. coindetii*, its impact on the North Sea food web will probably increase and therefore also its potential to exert an impact on North Sea fish species.

Todaropsis eblanae—Lesser flying squid

Todaropsis eblanae is moderate abundant in the IBTS samples (de Heij and Baayen 2005; Oesterwind et al. 2010). In ten of ten stomachs of *T. eblanae* sampled in the central North Sea, fish remains (e.g. *S. sprattus* in one stomach) and unidentified cephalopod items were found (Zumholz 2001). Another study described *Trisopterus* sp., Gobiidae and again *S. sprattus* as fish prey (Schroeder 1999). Fish make up the main part of the diet, whereas cephalopods and crustaceans play a minor role in samples from IBTS surveys, with the proportion of crustaceans in prey of *T. eblanae* decreasing with an increase in DML (Form and Oelschlägel 2004). Clupeidae, Argentinidae, Gadidae and Ammodytidae form the bulk of the fish prey with *Argentina silus* (9 times), *C. harengus* (6 times), *G. argenteus* (4 times), *S. sprattus* (3 times) and *Alosa. fallax* (1 time) at the species level (Form and Oelschlägel 2004). In conclusion, the combination of moderate abundances of *T. eblanae* and the high proportion of fish items in its prey make it very likely that *T. eblanae* exerts a feeding pressure on commercially important fish species.

Todarodes sagittatus—European flying squid

The ommastrephid *T. sagittatus* is rare in IBTS samples (Oesterwind et al 2010). *T. sagittatus* is generally described as an opportunistic and aggressive predator (Breiby and Jobling 1985). In the Northeast Atlantic, it feeds on young *C. harengus* and *G. morhua* particularly frequently, and cannibalism has also been observed (Breiby and Jobling 1985; Joy 1990). In neighbouring seas of the North Sea, however, *T. sagittatus* can occur in high numbers (Breiby and Jobling 1985; Oesterwind et al. 2015) and it might have the potential to increase in abundance in the North Sea within the near future.

Others

Only low numbers of *E. cirrhosa* occur in the IBTS (de Heij and Baayen 2005; Oesterwind et al 2010). Other studies describe decapods as the main food (Boyle 1983, 1986; Pierce et al. 2010; Jereb et al. 2015). The results suggest, that *E. cirrhosa* very likely does not exert a top-down effect on commercially important fish species.

In addition to our findings, Yau (1994) describes mysidaceans and decapods as food for *S. atlantica* that are usually caught near the seabed during dawn or dusk. Feeding on fish eggs cannot be excluded, but it is likely that *S. atlantica* has little or no direct predatory impact on fish in general.

S. oweniana mainly feeds on crustaceans (Reid and Jereb 2005). As this species is a relatively small cephalopod and only Gobiidae were identified amongst the fish prey in the North Sea, it can be assumed that *S. oweniana* has a low impact on commercially used fish species.

Due to the rare occurrence of *R. macrosoma* within the IBTS samples (de Heij and Baayen 2005; Oesterwind et al. 2010), we assume that *R. macrosoma*, unless it eats fish eggs of commercially exploited species, has no direct top-down influence on corresponding fishes.

The same can be assumed for the cuttlefishes *S. elegans* (two specimens collected) and *S. officinalis* (one specimen collected; de Heij and Baayen 2005; Oesterwind et al. 2010). *S. elegans* is described as a small efficient predator that eats small fish, crustaceans and polychaetes (Reid and Jereb 2005). Unlike many other species, this species shows no correlation between DML and prey composition in samples from the Ria de Vigo, off Northwest Spain (Guerra 1985; Castro and Guerra 1990). There, *S. officinalis* feeds mainly on crustaceans, demersal fish, cephalopods and polychaetes. Its prey composition depends on body size, so that crustaceans occupy a more important position in the diet of smaller cuttlefish, and fish become more important with increasing size. In addition, cannibalism has been described for all sizes (Guerra 1985; Castro and Guerra 1990). Due to the low numbers of both species in the North Sea, we assume that they have no major impact on commercially exploited fish species, but probably a local impact, e.g. at *S. officinalis* spawning sites in the southern North Sea like the English Channel.

Conclusion

The current study provides basic information for a North Sea food web model and illustrates the wide dietary spectrum of North Sea cephalopods. Especially larger squids like *L. forbesii*, *L. vulgaris* and all ommastrephids feed on a broad spectrum of fish species including different commercially used species whilst smaller individuals mainly feed on crustaceans. However, some smaller squids such as *Alloteuthis* spp. prey on Gobiidae and commercially used species like Clupeidae. Furthermore, fish eggs have not been considered as cephalopod prey in recent studies, but their consumption by cephalopods can have substantial impacts on the recruitment of commercially valuable fish species. Our study emphasizes that due to an increasing biomass of various North Sea cephalopods (van der Kooij et al. 2016; Oesterwind et al 2022), their impact within the North Sea food web has increased and that large-sized cephalopods have become more important as predators for fish including commercially used species. Further monitoring of North Sea cephalopods and studies on their trophic ecology are necessary for a better evaluation of their impact within the North Sea food web to facilitate an ecosystem-based fisheries management in the future.

Acknowledgements We thank the Thünen Institute of Sea Fisheries with the support of cephalopod sampling within the last years, Heinz Brendelberger for his general support during the sampling and inspiration, as well as for the application of the project in which the sampling occurred and two reviewers for their constructive critics that improved the manuscript.

Author contribution DO design, funding acquisition, field work, lab work, writing first draft, leading revision. UP design, revised first draft and revision.

Funding Open Access funding enabled and organized by Projekt DEAL. This study was partly funded by the German Environmental Foundation (Deutsche Bundesstiftung Umwelt, DBU).

Data availability The dataset used for the case study is available by the corresponding author on reasonable request.

Declarations

Conflict of interest There is no conflict of interest or competing interest.

Ethics approval All species are not protected under any legislation and not considered threatened or endangered. Samples were bycatch during ICES coordinated international fishing trawl surveys. The Thünen Institute has the experience and permission for fishing within the study areas and is particularly committed to ethical values when dealing with living animals. The Thünen Institute follows the following fundamental principles: 1- keep the sampling effort to the minimum needed to accomplish the research tasks; 2- keep stress for the sampled animals as low as possible.

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